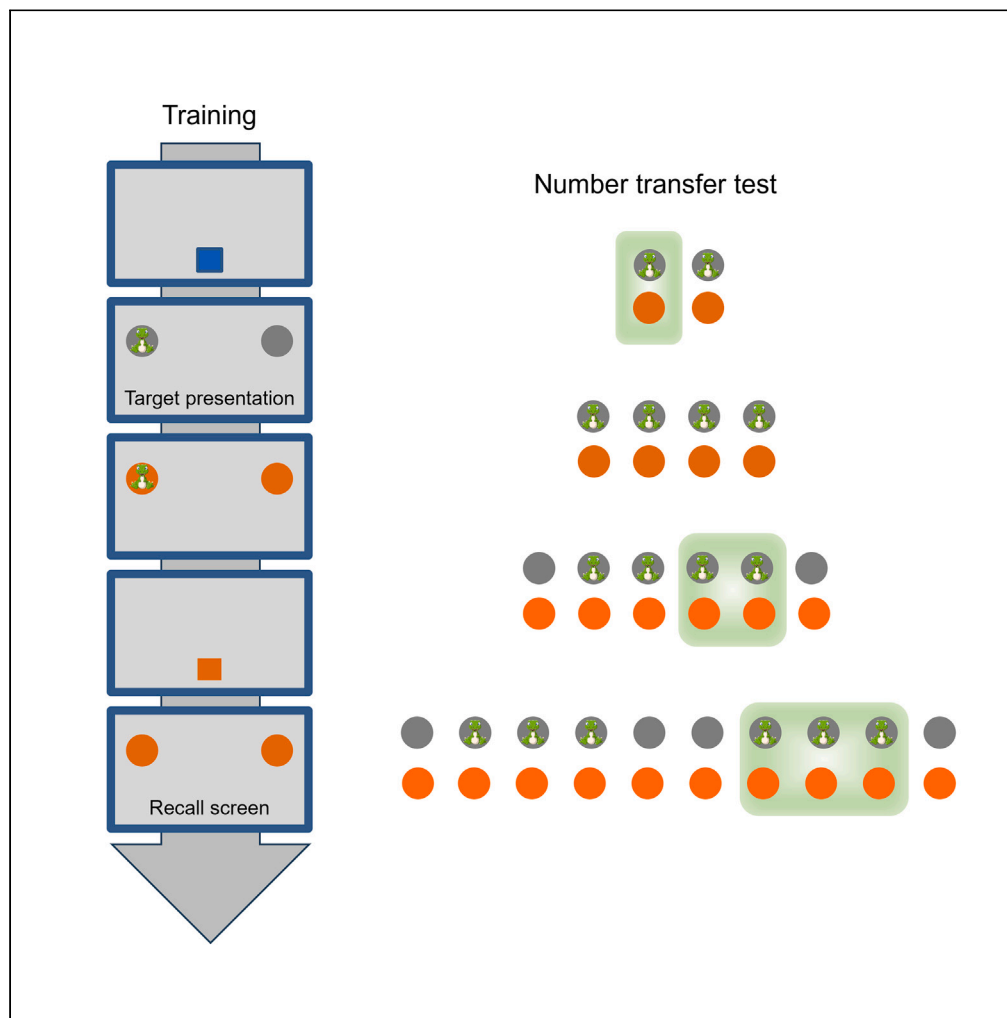


Article

Magnitude shifts spatial attention from left to right in rhesus monkeys as in the human mental number line



Rosa Rugani,
Michael L. Platt,
Yujia Zhang,
Elizabeth M.
Brannon

rosa.rugani@unipd.it

Highlights

Monkeys learn to memorize the location of a target on one of two lateral dots

Monkeys perform accurately with novel arrays of 2, 4, 6, or 10 dots

Monkeys remember better left targets with 2 dots, and right targets with 6 or 10 dots

Monkeys show space-number association that resembles the mental number line

Rugani et al., iScience 27, 108866
February 16, 2024 © 2024 The Author(s).
<https://doi.org/10.1016/j.isci.2024.108866>



Article

Magnitude shifts spatial attention from left to right in rhesus monkeys as in the human mental number line

Rosa Rugani,^{1,2,7,*} Michael L. Platt,^{2,3,4} Yujia Zhang,^{5,6} and Elizabeth M. Brannon²

SUMMARY

Humans typically represent numbers and quantities along a left-to-right continuum. Early perspectives attributed number-space association to culture; however, recent evidence in newborns and animals challenges this hypothesis. We investigate whether the length of an array of dots influences spatial bias in rhesus macaques. We designed a touch-screen task that required monkeys to remember the location of a target. At test, monkeys maintained high performance with arrays of 2, 4, 6, or 10 dots, regardless of changes in the array's location, spacing, and length. Monkeys remembered better left targets with 2-dot arrays and right targets with 6- or 10-dot arrays. Replacing the 10-dot array with a long bar, yielded more accurate performance with rightward locations, consistent with an underlying left-to-right oriented magnitude code. Our study supports the hypothesis of a spatially oriented mental magnitude line common to humans and animals, countering the idea that this code arises from uniquely human cultural learning.

INTRODUCTION

Representing spatial information is crucial for survival in most animals.^{1–3} The spatial organization of mental representations is intrinsic to many abstract arbitrary classifications, such as numerical and non-numerical ordinal information in humans^{2,4–6} and animals.^{7–9} A great deal of evidence suggests that numbers are organized from left to right on what is often called a “mental number line” in humans.^{5,10} For example, adults are faster in making parity judgments about small numbers when responses are executed on the left and making parity judgments about large numbers when responses are executed on the right (spatial-numerical association of response codes, SNARC effect¹¹).

When first reported, the orientation of the mental number line was hypothesized to be an outcome of formal instruction. From this perspective, spatial-numerical mapping is a by-product of culture, arising from reading and writing conventions and the use of tools such as rulers.¹² Consistent with this idea, Arabic speakers who read from right to left show an inverted SNARC effect,¹³ whereas cultures with mixed reading habits (i.e., where reading is right-to-left but number is represented from left-to-right) show no SNARC effect.¹⁴ However, recent studies suggest that spatial numerical associations (SNA) do not arise solely from cultural practices because they are evident in infants before they learn to read or write. In one study, seven-month-old infants looked longer at increasing (e.g., 1-2-3) but not at decreasing (e.g., 3-2-1) magnitudes displayed in a left-to-right spatial orientation.¹⁵ Similarly, eight-month-old infants, initially presented with a central numerosity and then with a peripheral target that could appear either on the left or on the right, were faster at orienting toward left targets when the cue numerosity was small (two dots) and toward right targets when the cue numerosity was large (nine dots).¹⁶ Even more surprisingly, newborns also appear to associate numerosities with a left-to-right-oriented mental number line. After being habituated to 12 dots, newborns were presented with two identical arrays of dots, one on the left and one on the right side of the screen. When the arrays both contained four dots, the newborns looked longer at the left stimulus, whereas when both arrays contained 36 dots newborns looked longer at the right array. Furthermore, when tested with two arrays of 12 dots, newborns preferred the left array if they were habituated with 36 items, but the right array if they were habituated to 4 items.¹⁷ Thus, for newborns habituation to a numerical magnitude becomes a reference against which subsequent magnitudes are spontaneously compared. Such data from newborns and infants in the first year of life suggests that number-space mappings are not solely driven by cultural practices but instead reflect the intrinsic organization of an underlying code for magnitude.

¹Department of General Psychology, University of Padua, Padua, Italy

²Department of Psychology, School of Arts and Sciences, University of Pennsylvania, Philadelphia, PA, USA

³Department of Neuroscience, Perelman School of Medicine, University of Pennsylvania, Philadelphia, PA, USA

⁴Marketing Department, The Wharton School, University of Pennsylvania, Philadelphia, PA, USA

⁵Department of Developmental Psychology and Socialization, University of Padua, Padua, Italy

⁶Department of Psychology, The Ohio State University, Columbus, OH 43210, USA

⁷Lead contact

*Correspondence: rosa.rugani@unipd.it
<https://doi.org/10.1016/j.isci.2024.108866>



Additional evidence for an intrinsic biological origin of the spatial numerical association comes from studies in animals. In one study, day-old domestic chicks were trained to select the 4th container in a vertically oriented array of ten identical containers for food reward. The chicks were then tested with an identical array rotated by 90°. Even though the birds entered the arena in the middle of the horizontal array of containers, they selected the 4th container on the left more than the 4th container from the right or any other location.¹⁸ These findings suggest chicks have an intrinsic bias to represent number from left to right. Similar results were obtained when adult Clark's nutcrackers,¹⁹ adult rhesus monkeys,²⁰ and children²¹ were tested using the same general paradigm. These findings suggest that when animals learn a numerical rule, they spontaneously organize the information from left to right. An alternative possibility, however, is that these findings reflect pseudo-neglect—a bias to attend more to objects on the left than the right^{22–24}—which has been observed in humans²⁵ and birds.^{26,27}

A noteworthy aspect of human number-space mappings is that they are relative rather than absolute. Specifically, the range of numerosities presented determines whether a given value is considered small or large. Thus when humans are tested with values in the 1–9 range they respond faster when 9 is on the right, but when tested with values in the 9–18 range, responses are faster when 9 is on the left.⁵ Orangutans and gorillas have shown relative numerical bias in spatial responses as well.²⁸ Despite individual differences, overall apes showed spatial-numerical mappings that inverted when the cue indicated the opposite numerical response, consistent with accessing relative rather than absolute spatial representations of number. Relative mapping has been observed in other species as well. Three-day-old domestic chicks, initially trained to associate a reward with number 5, associated values less than 5 (i.e., 2) with the left and values larger than 5 (i.e., 8) with the right. Remarkably, when the rewarded value was 20 rather than 5, the chicks oriented to the left when 8 items were presented.²⁹ Using similar paradigms other research found different outcomes. Some studies reported no evidence of spatial number mapping in cleaner fish, rhesus monkeys and capuchin monkeys.^{30,31} Additional studies in newborns,^{17,32} day-old chicks,³³ and honeybees³⁴ revealed both bidirectionality and relativity of spatial-numerical associations, two main features of the adult human mental number line. The bidirectional aspect is derived from small numbers biasing responses to the left and large numbers biasing responses to the right. In these studies, reference numerosity modulated the numerical displacement depending on its relative magnitude, with the test number eliciting responses indicative of relative mapping. Overall, these findings suggest the use of space to represent other dimensions is both common across animal species^{35,36} and based on developmentally primitive biological mechanisms, but can be influenced by experience.

Despite considerable evidence from behavioral studies, the neural basis of the SNA remains poorly understood. One account posits that the spatial organization of number observed in response biases reflects the orientation of spatial attention.^{11,37} In humans and monkeys, the intraparietal sulcus (IPS) is involved in the representation of numerals and numerosities,^{38–41} as well as in space perception and spatial attention (for a review, see studies by Hubbard et al., and Piazza et al.,^{42,43}). Neurons selective to numerosities have been found in parietal and prefrontal cortex in monkeys.⁴⁴ In birds, neurons selective to numerosities have been observed in the association area *Nidopallium caudolaterale* (NCL), a brain area possibly homologous with mammalian cortex, in both the crow⁴⁵ and the chick.⁴⁶ In humans, populations of neurons tuned to small numerosities are organized topographically in the parietal cortex, thereby forming a map,^{47,48} which may underlie the spatial organization of magnitudes. Together, this evidence suggests that direction of attention along the mental number line and spatial numerical association may jointly arise from the neural mechanisms supporting the orienting of spatial attention.^{49,50}

Nevertheless, to explain the SNARC effect, numerical magnitude must be processed before triggering spatial associations,^{51–54} as shown by an event-related potentials (ERPs) study.⁵⁵ Participants, while engaged in a target detection task, were presented with non-predictive and task-irrelevant arrows and numerals. The modulation of the P2p component, reflecting semantic number processing,⁵⁶ occurred prior to the interactions between numerical magnitude and hemisphere over parietal sites, reflecting shifts of attention induced by number cues (for similar results in EEG, rTMS, fMRI studies, see studies by Gobel S.M et al., Dehaene et al., and Mora-Cortes et al.,^{57–59}). Remarkably, both arrows and numerals elicited two ERP components—the “early directing attention negativity” (EDAN) and the “anterior directing attention negativity” (ADAN)—that reflect the activity of the fronto-parietal attentional network engaged in the control of spatial attention.^{60,61} The EDAN and ADAN, in turn, modulated early ERP responses (P1 and N1 components) to the targets, suggesting that the same fronto-parietal networks involved in volitional shifts of attention are also engaged in reflexive endogenous shifts of attention.⁵⁵

Despite increasing evidence supporting an intrinsic association between numerosity and space that is common to vertebrates, evidence for the flexibility of this association and whether it is specific to discrete magnitudes or whether it also applies to continuous extents remains sparse. To address these gaps, we designed a new touch screen task to explore whether rhesus monkeys show a flexible side bias in an ordinal target selection task. The task required remembering the ordinal position of a target in an array of identical discrete elements. This paradigm excluded odor cues or experimenter influence and allowed precise control over the spatial placement of visual stimuli, enabling us to disentangle the use of ordinal numerical from purely spatial cues. We first trained rhesus monkeys to select a target (a picture of a green dinosaur) that appeared on one of two identical dots (Figure 1). Next, we required monkeys to remember the location of the target and to select the dot on which the target had previously appeared. To ensure that monkeys were not learning the absolute spatial location of the target, the array was jittered vertically across trials, by varying its dislocation on the vertical axis by 8 cm.

After monkeys were trained to identify the left or right target, we tested whether they could remember the location of the target on 2, 4, 6, or 10 dot arrays and asked how numerical magnitude affected their accuracy at selecting the correct target location. If a left-to-right displacement induces a unilateral leftward attentional shift, they should perform better when targets were presented on the leftward dots than on the rightward dots. Furthermore, if the numerical length of an array influences the locus of visuo-spatial attention, then monkeys should perform better for left targets on numerically small arrays and right targets on numerically large arrays.

To disentangle whether monkeys used spatial versus ordinal strategies to encode the target location, we employed a conflict test. Here, we changed the physical distance between the dots during the presentation and recall phases, to ensure that the absolute spatial location and

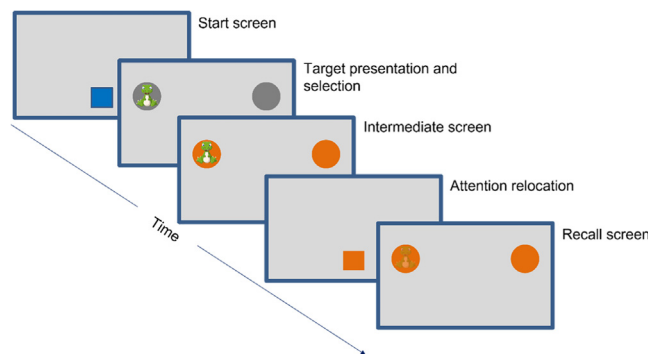


Figure 1. Schematic illustration of the screen succession in the training procedure as in Training 3

A training trial started with the presentation of a blue response square; once selected, two dark gray dots appeared. The target stimulus, a green dinosaur, appeared on either dot. When the target was selected, the two dots turned orange for 3 s before disappearing. A horizontally centered orange response square appeared in the bottom area of the monitor. This always appeared in the same position to direct monkey attention to the same part of the monitor. Once the orange response square was selected, two orange dots appeared and the target stimulus could be visible, depending on training phase, on the same dot in which it appeared in the previous screens (in this illustration the target was faded as in some trials of the second phase of Training 3). The selection of the dot on which the target was presented elicited a positive reward.

the correct numerical target were not the same. During the presentation phase, the target always appeared on the 3rd dot out of 6 dots. However, during the recall phase of each trial, the distance between the dots was reduced such that the 3rd dot from the left would be chosen if monkeys used numerical order to respond, whereas the 2nd dot from the left would be chosen if they used the absolute spatial location of the original target.

Finally, we tested whether monkeys would transfer training on arrays of discrete items to continuous stimuli. The target appeared at specific location on an unsegmented line in the presentation phase and monkeys were required to touch on the same unsegmented line in the recall phase. If spatial bias is solely due to an underlying number-space mapping, there should be no left-to-right bias in performance in this non-numerical version of the task. Alternatively, if spatial mapping is common to all magnitudes, then monkeys should show the same spatial biases to arrays of dots and unsegmented lines.

RESULTS

Number transfer test

As shown in Table 1, both monkeys selected the ordinaly correct dot above chance levels in all number transfer tests (binomial tests, all $p < 0.001$; more data are available in Table S1).

We next examined data from each experiment separately to better understand the monkeys' accuracy in identifying each target and to determine if there was any bias in their lateral response patterns (left vs. right) (Figure 2). First, we performed Binomial tests, separately for each monkey, on the average accuracy for each target position in each test against chance levels (detailed statistics can be found in Table S1). Next, Wilcoxon tests were conducted on the accuracy as a function of target side after aggregating targets on the same side (for example, in the 4-dot test, 1L and 2L were considered as left and 1R and 2R were considered as right).

Two-dot test

In the two-dot test, Hooke remembered both 1L and 1R above chance (1L, mean accuracy = 91.667, SE = 4.672, $p < 0.001$; 1R, mean accuracy = 69.444, SE = 7.786, $p = 0.014$; see more statistics in Table S1) while Sally only successfully recalled 1L (1L, mean accuracy = 94.444, SE = 3.872, $p < 0.001$; 1R, mean accuracy = 63.889, SE = 8.119, $p = 0.066$). Both monkeys performed better at recalling the left target (Hooke, left = 91.667, SE = 4.672, right = 69.444, SE = 7.786, $W = 792$, $p = 0.018$, $r = 0.279$; Sally, left = 94.444, SE = 3.872, right = 63.889, SE = 8.119, $W = 846$, $p = 0.002$, $r = 0.374$).

Four-dot test

In the 4-dot test, Hooke successfully recalled the right but not left target positions (1L, mean accuracy = 14.815, SE = 6.967, $p = 0.933$; 2L, mean accuracy = 22.222, SE = 8.153, $p = 0.701$; 2R = 71.429, SE = 8.694, $p < 0.001$; 1R, mean accuracy = 83.333, SE = 6.920, $p < 0.001$). Sally successfully identified all the target positions significantly above chance (1L, mean accuracy = 55.556, SE = 8.399, $p < 0.001$; 2L, mean accuracy = 88.889, SE = 5.312, $p < 0.001$; 2R, mean accuracy = 69.444, SE = 7.786, $p < 0.001$; 1R, mean accuracy = 63.889, SE = 8.119, $p < 0.001$). In terms of side bias, Hooke performed better on the right side while Sally showed no difference (Hooke, left = 18.519, SE = 5.336, right = 77.586, SE = 5.523, $W = 641$, $p < 0.001$, $r = 0.588$; Sally, left = 72.222, SE = 5.316, right = 66.667, SE = 5.595, $W = 2736$, $p = 0.472$, $r = 0.060$).

Table 1. The accuracy of each monkey in each experiment of the number transfer test

| subject | experiment | correct N | total N | chance % | Mean accuracy% | SEM | p | Cohen h |
|---------|------------|-----------|---------|----------|----------------|-------|--------|---------|
| Hooke | two-dot | 58 | 72 | 50 | 80.556 | 4.697 | <0.001 | 2.087 |
| | four-dot | 55 | 112 | 25 | 49.107 | 4.745 | <0.001 | 1.453 |
| | six-dot | 58 | 144 | 16.667 | 40.278 | 4.101 | <0.001 | 1.293 |
| | ten-dot | 53 | 211 | 10 | 25.118 | 2.993 | <0.001 | 0.987 |
| Sally | two-dot | 57 | 72 | 50 | 79.167 | 4.820 | <0.001 | 2.052 |
| | four-dot | 100 | 144 | 25 | 69.444 | 3.852 | <0.001 | 1.870 |
| | six-dot | 75 | 144 | 16.667 | 52.083 | 4.178 | <0.001 | 1.531 |
| | ten-dot | 80 | 215 | 10 | 37.209 | 3.304 | <0.001 | 1.249 |

Six-dot test

In the 6-dot test, Hooke again succeeded in identifying targets on the right but not on the left (2L, mean accuracy = 19.444, SE = 6.690, $p = 0.393$; 3L, mean accuracy = 22.222, SE = 7.027, $p = 0.243$; 3R = 36.111, SE = 8.119, $p = 0.004$; 2R = 83.333, SE = 6.299, $p < 0.001$). Sally selected the right targets and 3L above chance expectations (2L, mean accuracy = 2.778, SE = 2.778, $p = 0.999$; 3L, mean accuracy = 44.444, SE = 8.399, $p < 0.001$; 3R = 80.556, SE = 6.690, $p < 0.001$; 2R = 80.556, SE = 6.690, $p < 0.001$). Both monkeys showed higher accuracy for targets on the right than for those on the left (Hooke, left = 20.833, SE = 4.820, right = 59.722, SE = 5.821, $W = 1584$, $p < 0.001$, $r = 0.395$; Sally, left = 23.611, SE = 5.040, right = 80.556, SE = 4.697, $W = 1116$, $p < 0.001$, $r = 0.568$).

Ten-dot test

In the 10-dot test, Hooke succeeded in remembering 2R, 3R, and 4L (2L, mean accuracy = 14.706, SE = 6.165, $p = 0.250$; 3L, mean accuracy = 20.000, SE = 6.860, $p = 0.055$; 4L, mean accuracy = 27.778, SE = 7.571, $p = 0.002$; 4R, mean accuracy = 20.000, SE = 6.860, $p = 0.055$; 3R, mean accuracy = 25.714, SE = 7.495, $p = 0.006$; 2R, mean accuracy = 41.667, SE = 8.333, $p < 0.001$). Sally remembered all targets except for 2L (2L, mean accuracy = 2.778, SE = 2.778, $p = 0.977$; 3L, mean accuracy = 22.222, SE = 7.027, $p = 0.024$; 4L, mean accuracy = 38.889, SE = 8.240, $p < 0.001$; 4R, mean accuracy = 50.000, SE = 8.452, $p < 0.001$; 3R = 63.889, SE = 8.119, $p < 0.001$; 2R = 45.714, SE = 8.543, $p < 0.001$). Hooke did not show differences between left and right, while Sally performed better when identifying right targets (Hooke, left = 20.952, SE = 3.991, right = 29.245, SE = 4.439, $W = 5103.5$, $p = 0.166$, $r = 0.096$; Sally, left = 21.296, SE = 3.958, right = 53.271, SE = 4.846, $W = 3930.5$, $p < 0.001$, $r = 0.330$; [Figure 2](#)).

To examine accuracy as a function of numerosity for left and right targets we conducted binomial GLMs on response outcomes (1 = correct or 0 = incorrect) as a function of the target side (left or right) and the number of dots (2, 4, 6, or 10) for each subject ([Figure 3](#)). Hooke showed a main effect of number of dots, with accuracy decreasing as number increased ($\chi^2 = 72.141$, $df = 3$, $p < 0.001$), as well as an interaction between side and number ($\chi^2 = 38.801$, $df = 3$, $p < 0.001$). Pairwise comparisons with the Bonferroni correction revealed a left bias in 2-dot, right bias in 4-dot and 6-dot and no bias in 10-dot (left versus right: two-dot, $z = 2.243$, $p = 0.025$; four-dot, $z = -5.782$, $p < 0.001$; six-dot, $z = -4.589$, $p < 0.001$; ten-dot, $z = -1.384$, $p = 0.166$). Sally showed a main effect of side ($\chi^2 = 24.094$, $df = 1$, $p < 0.001$), a main effect of number of dots ($\chi^2 = 103.651$, $df = 3$, $p < 0.001$), and an interaction between side and number ($\chi^2 = 56.823$, $df = 3$, $p < 0.001$). She showed a left bias in the 2-dot test, a right bias in the 6- and 10-dot tests, and no bias in the 4-dot test (left versus right: two-dot, $z = 2.807$, $p = 0.005$; four-dot, $z = 0.723$, $p = 0.4698$; six-dot, $z = -6.377$, $p < 0.001$; ten-dot, $z = -4.721$, $p < 0.001$; [Figure 3](#)).

Conflict test

To assess whether monkeys' choices were determined by the numerical ordinal position of the target or the spatial location of the target we conducted binomial tests on the percentage of choices for both ordinal-correct (3L or 3R, the ordinal positions in which the target appeared, [Figure 4, Target presentation](#)) and spatial-correct (2L or 2R, respectively, [Figure 4, Recall array](#)) locations against chance level (more data are available in [Table S2](#)).

First, we tested the use of spatial versus ordinal position, combining the two numerically correct options (3L and 3R) and the respective spatial correct options (2L and 2R). Both monkeys chose spatial-correct (2L or 2R) but not ordinal-correct (3L or 3R) options above chance (Hooke, ordinal-correct, mean accuracy = 20.833, SE = 4.897; $p = 0.211$, Cohen $h = 0.107$; spatial-correct, mean accuracy = 54.167, SE = 5.913, $p < 0.001$, Cohen $h = 0.813$; Sally, ordinal-correct, mean accuracy = 22.222, SE = 4.934; $p = 0.135$, Cohen $h = 0.141$; spatial-correct, mean accuracy = 58.333, SE = 5.851; $p < 0.001$, Cohen $h = 0.897$). Further proportional tests indicated that both monkeys relied on spatial position of the target more than the ordinal position of the target (Hooke: $\chi^2 = 15.674$, $df = 1$, $p < 0.001$, Cohen $h = 0.706$; Sally: $\chi^2 = 18.043$, $df = 1$, $p < 0.001$, Cohen $h = 0.756$).

Then we analyzed each target position separately. When the target appeared at 3L, Hooke chose 2L, which was spatially correct, above chance expectations, and did not choose 3L above chance expectations (3L, mean accuracy = 19.444, SE = 6.690; $p = 0.393$, Cohen $h = 0.072$; 2L, mean accuracy = 30.556, SE = 7.786; $p = 0.028$, Cohen $h = 0.330$). Sally chose both the numerical and spatial locations significantly above

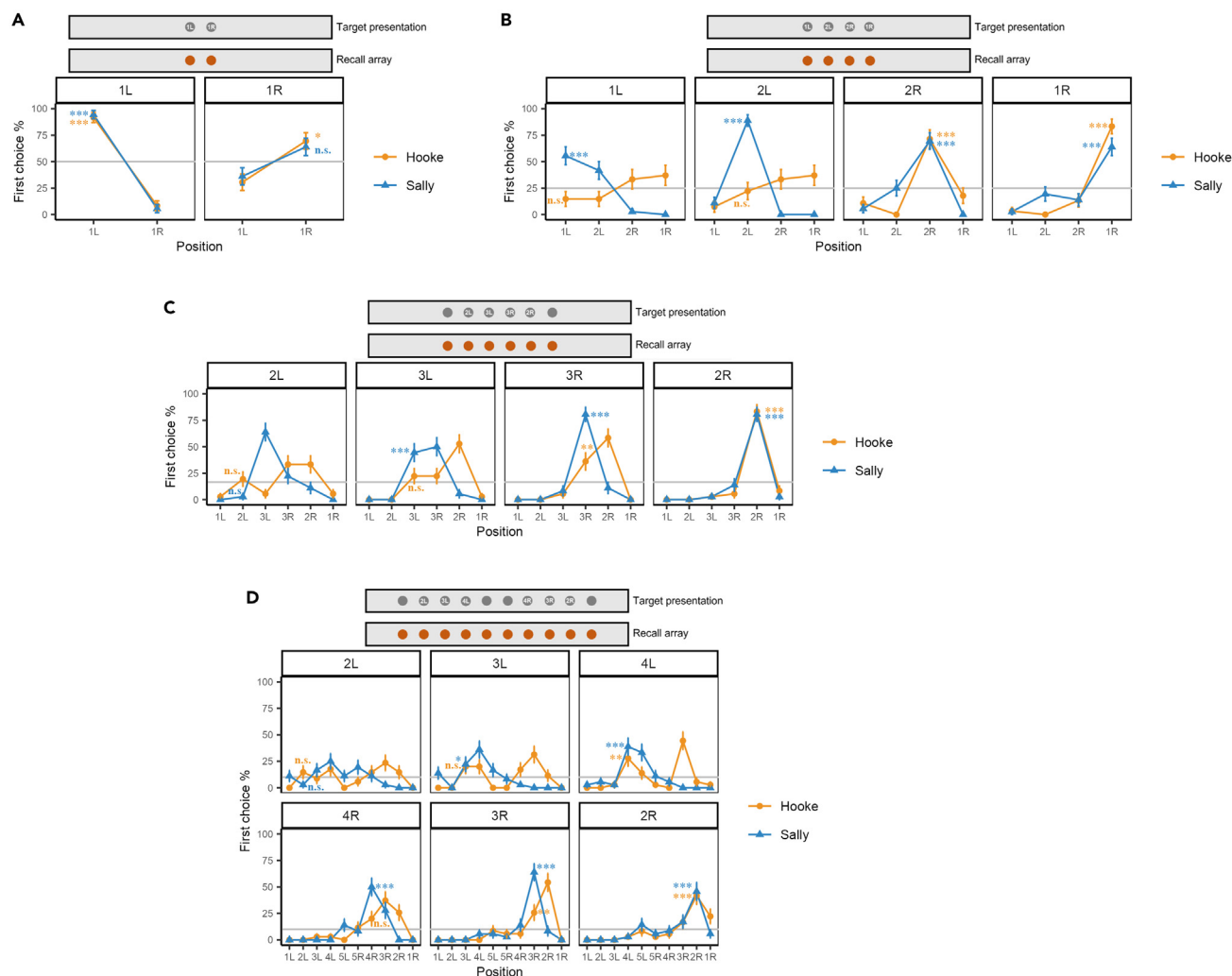


Figure 2. Percentage of choosing each position as a function of target position and subject in number transfer tests: 2-, 4-, 6-, 10-dot array

Error bars indicate standard errors. Gray lines = chance.

(A) Two-dot experiment. Target located in 1L or 1R. Chance = 50%.

(B) Four-dot experiment. Target located at 1L, 2L, 2R, or 1R. Chance = 25%.

(C) Six-dot experiment. Target located at 2L, 3L, 3R, or 2R. Chance = 16.667%.

(D) Ten-dot experiment. Target located in 2L, 3L, 4L, 4R, 3R, or 2R. Chance = 10%. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s. not significant.

chance expectations (3L, mean accuracy = 36.111, SE = 8.119; $p = 0.004$, Cohen $h = 0.448$; 2L, mean accuracy = 38.889, SE = 8.240; $p = 0.001$, Cohen $h = 0.506$). When the target appeared at 3R, both monkeys selected the spatially correct position (2R) significantly above chance expectations and did not choose the numerically correct position (3R) above chance expectations (Hooke, 3R, mean accuracy = 22.222, SE = 7.027; $p = 0.243$, Cohen $h = 0.141$; 2R, mean accuracy = 77.778, SE = 7.027; $p < 0.001$, Cohen $h = 1.319$; Sally, 3R, mean accuracy = 8.333, SE = 4.672; $p = 0.953$, Cohen $h = 0.255$; 2R, mean accuracy = 77.778, SE = 7.027; $p < 0.001$, Cohen $h = 1.319$; Figure 4).

To further understand how target locations influenced monkeys' responses, GLMs on the number of first choices as a function of position (1L, 2L, 3L, 3R, 2R, 1R) and target side (left vs. right) were conducted for each monkey using a Poisson distribution as the number of first choices is a counting variable. Hooke showed a main effect of position ($\chi^2 = 33.773$, $df = 5$, $p < 0.001$), no effect of target side ($\chi^2 = 0$, $df = 1$, $p = 1$) and an interaction between target position and side ($\chi^2 = 43.831$, $df = 5$, $p < 0.001$). When the target appeared on the left (3L), Hooke selected the six positions equally ($ps = 1$). When the target was presented on the right (3R), he selected 2R more than 3R ($z = 3.125$, $p = 0.027$; see Table S2), suggesting that the spatially correct position was chosen more than the ordinaly correct position. Sally showed a main effect of the target position ($\chi^2 = 38.818$, $df = 5$, $p < 0.001$), a main effect of side ($\chi^2 = 5.062$, $df = 1$, $p = 0.024$) and an interaction between the two ($\chi^2 = 61.458$, $df = 5$, $p < 0.001$). When the target appeared on the left (3L), the number of choices did not differ on each position ($ps > 0.1$). When the target was presented on the right (3R), she selected the spatially correct location (2R) more than any other ($ps < 0.05$). No other significant differences were observed ($ps = 1$).

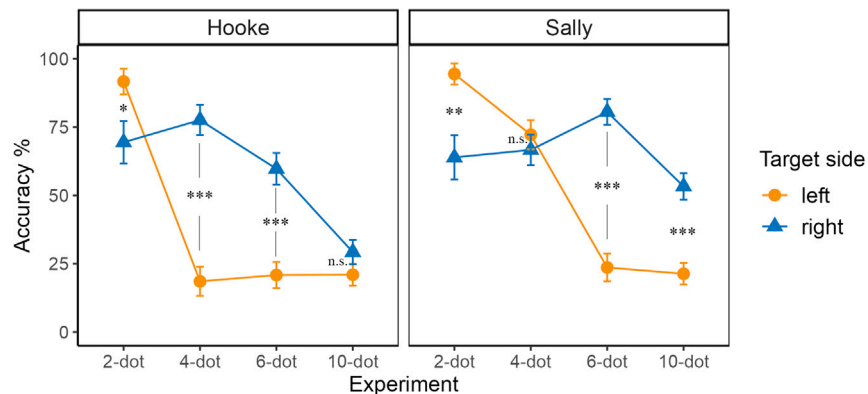


Figure 3. Monkeys' accuracy in number transfer tests on each side
Asterisks indicate significant difference between left versus right targets. Error bars = SEMs. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Continuous transfer test

As shown in Figure 5, both monkeys performed above the chance expectation in the continuous transfer test (Hooke, mean accuracy = 23.148, SE = 2.877, $p < 0.001$, Cohen $h = 0.360$; Sally, mean accuracy = 29.630, SE = 3.114, $p < 0.001$, Cohen $h = 0.507$). Both monkeys showed better accuracy when the target was on the right than the left (Hooke: left, mean accuracy = 7.407, SE = 2.532; right, mean accuracy = 38.889, SE = 4.713, $W = 18227$, $p < 0.001$, $r = 0.234$; Sally: left, mean accuracy = 20.370, SE = 3.894, right, mean accuracy = 38.889, SE = 4.713, $W = 17366$, $p < 0.001$, $r = 0.267$; Figure 5; the mean accuracy in choosing each target position in the 10-dot number transfer test is also reported in Figure 2D).

Hooke succeeded in remembering 2R and 3R while all other locations were chosen at chance (2L: mean accuracy = 16.667, SE = 6.299; $p = 0.145$; 3L: mean accuracy = 2.778, SE = 2.778; $p = 0.977$; 4L: mean accuracy = 2.778, SE = 2.778; $p = 0.977$; 4R: mean accuracy = 19.444, SE = 6.690; $p = 0.063$; 3R: mean accuracy = 47.222, SE = 8.438; $p < 0.001$; 2R: mean accuracy = 50.000, SE = 8.452; $p < 0.001$). Sally remembered all the targets except for 2L (2L: mean accuracy = 13.889, SE = 5.846; $p = 0.289$; 3L: mean accuracy = 25.000, SE = 7.319; $p = 0.008$; 4L: mean accuracy = 22.222, SE = 7.027; $p = 0.024$; 4R: mean accuracy = 33.333, SE = 7.968; $p < 0.001$; 3R: mean accuracy = 44.444, SE = 8.399; $p < 0.001$; 2R: mean accuracy = 38.889, SE = 8.240; $p < 0.001$, see Table S1).

Comparison between continuous transfer test vs. 10-dot number transfer test

To better understand whether the lack of ordinal information afforded by a discrete array impaired monkeys' recall performance, binomial GLMs were conducted on each monkey separately on their accuracy (1 or 0) as a function of target positions (2L, 3L, 4L, 4R, 3R, 2R) and experimental condition (continuous transfer test versus ten-dot number transfer test; Figure 5, continuous transfer test; number transfer test). Hooke showed no main effects of target positions ($\chi^2 = 8.056$, $df = 5$, $p = 0.153$) nor of experimental condition ($\chi^2 = 0.051$, $df = 1$, $p = 0.822$). His responses displayed an interaction between target position and experimental condition ($\chi^2 = 19.623$, $df = 5$, $p = 0.001$). When the target was presented on 3L and 4L, he had higher accuracy in ten-dot test than in the continuous transfer test (3L: $z = 1.974$, $p = 0.048$; 4L: $z = 2.407$, $p = 0.016$). When looking at the effect of target position on each experiment, Hooke performed better in identifying 3R and 4R than 3L and 2L in continuous transfer test ($ps < 0.05$). Yet, there was no position effect in 10-dot number transfer test ($ps > 0.1$). No other significant results were observed for Hooke.

Sally only showed a main effect of target positions ($\chi^2 = 43.173$, $df = 5$, $p < 0.001$), but no effect of experimental condition ($\chi^2 = 3.154$, $df = 1$, $p = 0.076$) nor an interaction ($\chi^2 = 7.651$, $df = 5$, $p = 0.177$). Post hoc tests showed that her responses on 2L were less accurate than those on 2R, 3R, 4R, and 4L, and her responses on 3L were less accurate than those on 3R ($ps < 0.05$).

DISCUSSION

We investigated whether rhesus monkeys showed a side bias in a spatial/ordinal recall task. Specifically, we explored whether: (i) monkeys would transfer an ordinal position rule learned with 2-lateral items to new and longer arrays; (ii) array length influenced accuracy of leftward and rightward responses; (iii) monkeys spontaneously encoded the ordinal numerical position or the spatial position of targets; and (iv) monkeys trained to recall a target on an array of discrete items would transfer the general task demands when a target was presented on a continuous unsegmented line.

After training to identify which of two lateral identical dots briefly contained a target, monkeys maintained high performance recalling the target when tested with 2, 4, 6, or 10 dot arrays. Importantly, the numerosity of the arrays influenced accuracy and interacted with the laterality of the target. In the 2-dot array, both monkeys showed an asymmetry, with better accuracy when the target appeared on the left than on the right. As predicted, accuracy became increasingly biased toward the right when targets were presented on longer arrays. With 4-dot arrays,

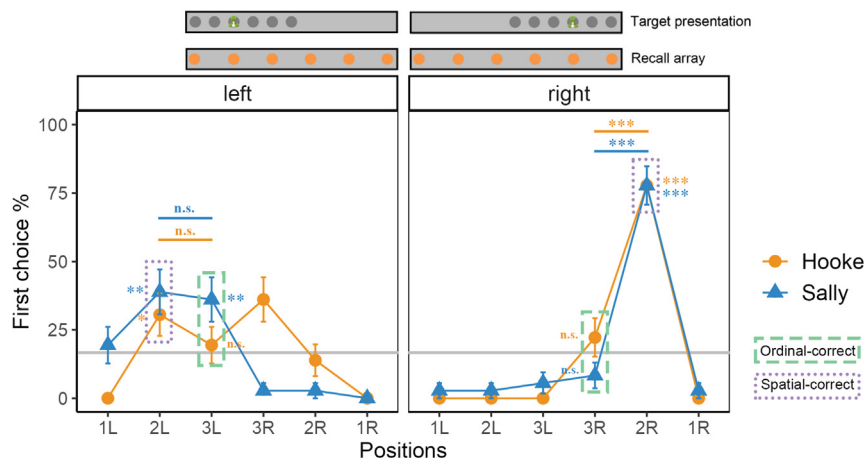


Figure 4. Percentage of first choices on each position in conflict tests

When the target was presented on the third left dot (3L), in the Recall phase, the ordinal-correct position was 3L while the spatial-correct position was 2L. When the target was presented on the third right dot (3R), in the Recall phase, the ordinal-correct position was 3R while the spatial-correct position was 2R. Error bars = SEMs. Gray lines = chance ($y = 16.667$). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Sally did not show any spatial bias, whereas Hooke was showed a bias toward better performance on right targets. Both monkeys performed better with right than left target locations when tested with the longer 6- and 10-dots arrays.

In a conflict test with 6-item arrays, we dissociated the numerical/ordinal and spatial cue to determine which dimension monkeys used to make their decisions. Monkeys continued to perform better when the target was presented on the right side, however, both monkeys relied more on spatial than numerical information. Future research may consider including control tests in which the number of dots varies while maintaining a constant length of the array, to disentangle the role of magnitude and numerosity in determining the side bias. The variability on the X axis affected monkeys' performance. However, when the arrays/dots were jittered vertically monkeys showed no changes in performance. It is possible that the horizontal plane is more meaningful than the vertical one for monkeys. Alternatively, the monkeys may have learned to ignore variations on the Y axis due to the jittered presentation along the vertical axis during training.

Finally in a continuous transfer test, we explored whether monkeys could generalize a rule learned over arrays of discrete stimuli to a continuously extended bar. Monkeys were presented with an unsegmented long bar and the target appeared in one of six spatial positions on the bar. Overall, monkeys performed above chance expectations and both monkeys were better at identifying targets on the right side than on the left. Such a cross-dimensional transfer from discrete to continuous dimensions, yet up to now poorly investigated—has also been reported in honeybees and implies a common and abstract magnitude code.⁶² Future studies should vary line length to determine the impact on spatial biases.

Our main finding was that as the number of dots increased, accuracy shifted from being better on the left to better on the right. This finding parallels data from children who showed better memory for left than right target positions (the cup under which a toy was hidden, in an array of ten horizontally arranged cups).⁶³ Left targets were likely associated with a left-to-right searching and right ones with a right-to-left searching. Higher accuracy on the left was explained by a more efficient left-to-right searching strategy in conditions that favored initial anchoring of attention to the most leftward cup, from which children initiated searching for the target.⁶³ A visual processing advantage for the left space, supported by right hemispheric dominance, has been posited for processing global spatial-attentional⁶⁴ and quantity processing in infants⁶⁵ and newborns.⁶⁶ A left-to-right oriented attentional bias is especially pronounced when adults were asked to name the midpoint of numerical intervals without calculating,^{49,50,57,67,68} and in ordinal tasks, in which Clark's nutcrackers, domestic chicks,¹⁹ monkeys,²⁰ and children²¹ were required to identify always a specific position, e.g., the 4th. It is plausible that ordinal tasks promoting the identification of an item in a constant array of discrete items on the basis of its spatial/ordinal position facilitate left-to-right oriented searching.^{19–21,63,69} On the other hand, shifts in behavioral responses from left to right occur only when numerosity and magnitude change. For instance, animals^{29,33,34} and newborns^{17,32} habituated to a specific numerosity displayed a left bias when faced with a new, smaller numerosity, but showed a right bias when presented with a larger numerosity.¹⁷ Our evidence builds upon and extends these findings and is consistent with the hypothesis that magnitude shapes performance by shifting attention to the left for smaller magnitudes and to the right for larger magnitudes (16,17,29,30,34) (for consistent evidence in humans, see studies by Ranzini et al., and Dehaene et al.,^{55,58}). This hypothesis can be tested in future experiments by using arrays containing a fixed or variable number of items. Fixed item arrays would elicit constant processing, while variable item arrays would induce flexible processing, leading in turn to either a unilateral (left-to-right or right-to-left oriented) or a bilateral (e.g., small on the left and large on the right) space-magnitude association. Although studies on human and animal mental number line have often focused on the horizontal plane, recent evidence in humans has shown that SNA also exist in the vertical plane.^{70,71} Our paradigm provides a valuable approach to explore both horizontal and vertical spatial numerical association in non-human animals.

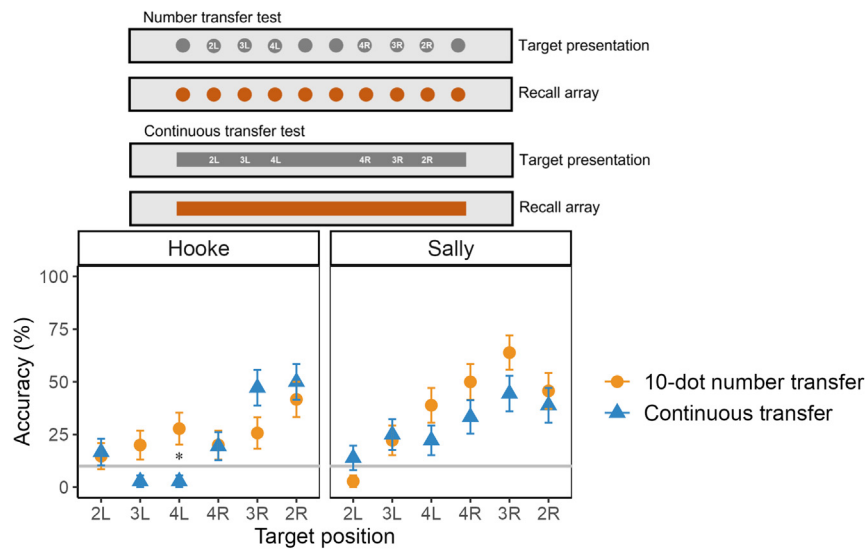


Figure 5. Mean accuracy in choosing each target position in the 10-dot number transfer test and the continuous transfer test
Error bars = SEMs. Gray lines = chance ($y = 10$). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

In our study, performance on small numerical arrays was consistent with a shift of attention toward the left and performance on larger numerical and spatial extents was consistent with a shift of attention toward the right (as shown in humans).^{37,55,57,59} Thus, our data cannot be entirely explained by a generalized allocation of spatial attention, known as “pseudoneglect” in humans²⁵ and birds^{26,27} that would result in biased attention to objects on the left. Instead, performance of monkeys shifted from left to right, depending on the extent of the array: small arrays elicited performance consistent with attention to the left, while performance on large arrays was consistent with attention to the right.

In conclusion, here we provide the first demonstration in a memory task of a connection between magnitude processing and a shift in accuracy from left to right in non-human primates. Our empirical evidence is consistent with both the spatial numerical association and the spatial quantity association. The latter hypothesis is a general mechanism, independent of magnitude type, which assumes quantities are associated with spatial locations, as in the spatial quantity association of response codes, SQUARC effect.⁷² The SNARC (spatial numerical association of response codes) effect may be a specific case of the more general SQUARC effect, which reflects a more general mapping between space and quantity that is not specific to number. Mappings onto space have been demonstrated for time,^{73–75} loudness,^{76–78} object size^{79,80} and weights,⁸¹ previously in humans, and for luminance in domestic chickens⁸² and humans.^{79,83} Our new demonstration of a magnitude-space mapping in a non-human primate invites the hypothesis that the interaction between these two types of magnitudes in human cognition reflects a shared, ancestral biological mechanism rather than a product of culture or a specific language. Thus, our findings support the view that the tendency to associate magnitude with space is not a cultural invention, but rather has deep developmental and evolutionary origins.

Limitations of the study

The current study focuses on the emergence of left vs. right bias in response to small or large magnitudes, respectively. Although the study also provides preliminary results on the transfer from discrete to continuous extents, the spatial bias is limited to a long continuous extent. While a similar right bias has been reported for long continuous extents and discrete arrays of dots, it does not address whether and how short continuous extents direct spatial bias. Furthermore, this study was conducted with only two subjects, and it would be insightful to test a larger sample size. One way that could be achieved is through multi-laboratory collaboration. Future work examining the association of continuous quantitative and discrete numerical extensions with left-right space could shed light on shared mechanisms underlying spatial quantitative and numerical associations.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
 - Lead contact
 - Materials availability
 - Data and code availability

- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
 - Subjects
- METHOD DETAILS
 - Apparatus, stimuli and procedure
 - Shaping
 - Shaping phase 1
 - Shaping phase 2
 - Shaping phase 3
 - Training
 - Training phase 1
 - Training phase 2
 - Training phase 3
 - Number transfer tests
 - Conflict test
 - Continuous transfer test
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2024.108866>.

ACKNOWLEDGMENTS

This material is based upon work supported by the European's Union Horizon 2020 Research and Innovation program under the Marie Skłodowska-Curie Grant/Award Number: 795242 to R.R.; PRIN 2022, grant/award number: 202254RHRT to R.R.; PRIN 2022 PNRR, grant/award number: P2022TKY7B, to R.R.; PRIN 2017: grant/award number: 2017PSRHPZ_003; and by NIH/NIMH grants (grant number R37MH109728 and R01MH108627) to M.P.

AUTHOR CONTRIBUTIONS

R.R., E.B., and M.P. designed the study; R.R. performed the experiments R.R. and Y.Z. analyzed the data; all authors discussed and interpreted the results; R.R. wrote the paper; Y.Z., M.P., and E.B. critically reviewed the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: October 18, 2023

Revised: November 21, 2023

Accepted: January 8, 2024

Published: January 11, 2024

REFERENCES

1. Gallistel, C.R. (1993). *The Organization of Learning*, 1st ed. (MIT Press).
2. Gevers, W., Reynvoet, B., and Fias, W. (2003). The mental representation of ordinal sequences is spatially organized. *Cognition* 87, B87–B95.
3. Butterworth, B. (2022). *Can Fish Count? what Animals Reveal about Our Uniquely Mathematical Minds*, First US edition (Basic Books).
4. Moyer, R.S., and Landauer, T.K. (1967). Time required for Judgements of Numerical Inequality. *Nature* 215, 1519–1520.
5. Dehaene, S. (2011). *The Number Sense: How the Mind Creates Mathematics Rev*, updated ed (Oxford University Press).
6. Previtali, P., de Hevia, M.D., and Girelli, L. (2010). Placing order in space: the SNARC effect in serial learning. *Exp. Brain Res.* 201, 599–605.
7. Merritt, D.J., and Terrace, H.S. (2011). Mechanisms of inferential order judgments in humans (*Homo sapiens*) and rhesus monkeys (*Macaca mulatta*). *J. Comp. Psychol.* 125, 227–238.
8. Brunamonti, E., Falcone, R., Genovesio, A., Costa, S., and Ferraina, S. (2012). Gaze orientation interferes with mental numerical representation. *Cognit. Process.* 13, 375–379.
9. Brunamonti, E., Genovesio, A., Carbè, K., and Ferraina, S. (2011). Gaze modulates non-propositional reasoning: further evidence for spatial representation of reasoning premises. *Neuroscience* 173, 110–115.
10. Galton, F. (1880). Visualised Numerals. *Nature* 21, 252–256.
11. Dehaene, S., Bossini, S., and Giraux, P. (1993). The mental representation of parity and number magnitude. *J. Exp. Psychol. Gen.* 122, 371–396.
12. Rugani, R., and de Hevia, M.-D. (2017). Number-space associations without language: Evidence from preverbal human infants and non-human animal species. *Psychon. Bull. Rev.* 24, 352–369.
13. Zebian, S. (2005). Linkages between Number Concepts, Spatial Thinking, and Directionality of Writing: The SNARC Effect and the REVERSE SNARC Effect in English and Arabic Monoliterates, Biliterates, and Illiterate Arabic Speakers. *J. Cognit. Cult.* 5, 165–190.
14. Shaki, S., Fischer, M.H., and Petrusic, W.M. (2009). Reading habits for both words and numbers contribute to the SNARC effect. *Psychon. Bull. Rev.* 16, 328–331.
15. de Hevia, M.D., Izard, V., Coubart, A., Spelke, E.S., and Streri, A. (2014). Representations of space, time, and number in neonates. *SA* 111, 4809–4813.
16. Bulf, H., de Hevia, M.D., and Macchi Cassia, V. (2016). Small on the left, large on the right: numbers orient visual attention onto space in preverbal infants. *Dev. Sci.* 19, 394–401.

17. Di Giorgio, E., Lunghi, M., Rugani, R., Regolin, L., Dalla Barba, B., Vallortigara, G., and Simion, F. (2019). A mental number line in human newborns. *Dev. Sci.* 22, e12801.
18. Rugani, R., Regolin, L., and Vallortigara, G. (2007). Rudimental numerical competence in 5-day-old domestic chicks (*Gallus gallus*): Identification of ordinal position. *J. Exp. Psychol. Anim. Behav. Process.* 33, 21–31.
19. Rugani, R., Kelly, D.M., Szelest, I., Regolin, L., and Vallortigara, G. (2010). Is it only humans that count from left to right? *Biol. Lett.* 6, 290–292.
20. Drucker, C.B., and Brannon, E.M. (2014). Rhesus monkeys (*Macaca mulatta*) map number onto space. *Cognition* 132, 57–67.
21. West, E., and McCrink, K. (2021). Eye Tracking Lateralized Spatial Associations in Early Childhood. *J. Cognit. Dev.* 22, 678–694.
22. Rugani, R., Vallortigara, G., Vallini, B., and Regolin, L. (2011). Asymmetrical number-space mapping in the avian brain. *Neurobiol. Learn. Mem.* 95, 231–238.
23. Rugani, R., and Regolin, L. (2020). Hemispheric specialization in spatial versus ordinal processing in the day-old domestic chick (*Gallus gallus*). *Ann. N. Y. Acad. Sci.* 1477, 34–43.
24. Rugani, R., Vallortigara, G., and Regolin, L. (2016). Mapping number to space in the two hemispheres of the avian brain. *Neurobiol. Learn. Mem.* 133, 13–18.
25. Jewell, G., and McCourt, M.E. (2000). Pseudoneglect: a review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia* 38, 93–110.
26. Diekamp, B., Regolin, L., Güntürkün, O., and Vallortigara, G. (2005). A left-sided visuospatial bias in birds. *Curr. Biol.* 15, R372–R373.
27. Regolin, L. (2006). The Case of the Line-Bisection: When Both Humans and Chickens Wander Left. *Cortex* 42, 101–103.
28. Gazes, R.P., Diamond, R.F.L., Hope, J.M., Caillaud, D., Stoinski, T.S., and Hampton, R.R. (2017). Spatial representation of magnitude in gorillas and orangutans. *Cognition* 168, 312–319.
29. Rugani, R., Vallortigara, G., Piffrits, K., and Regolin, L. (2015). Number-space mapping in the newborn chick resembles humans' mental number line. *Science* 347, 534–536.
30. Triki, Z., and Bshary, R. (2018). Cleaner fish *Labroides dimidiatus* discriminate numbers but fail a mental number line test. *Anim. Cogn.* 21, 99–107.
31. Beran, M.J., French, K., Smith, T.R., and Parrish, A.E. (2019). Limited evidence of number–space mapping in rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Sapajus apella*). *J. Comp. Psychol.* 133, 281–293.
32. de Hevia, M.D., Veggiotti, L., Streri, A., and Bonn, C.D. (2017). At Birth, Humans Associate “Few” with Left and “Many” with Right. *Curr. Biol.* 27, 3879–3884.e2.
33. Rugani, R., Vallortigara, G., Piffrits, K., and Regolin, L. (2020). Numerical magnitude, rather than individual bias, explains spatial numerical association in newborn chicks. *Elife* 9, e54662.
34. Giurfa, M., Marcourt, C., Hilpert, P., Thevenot, C., and Rugani, R. (2022). An insect brain organizes numbers on a left-to-right mental number line. *USA* 119, e2203584119.
35. Brugger, P. (2015). Chicks with a number sense. *Science* 347, 477–478.
36. Vallortigara, G. (2017). Comparative cognition of number and space: the case of geometry and of the mental number line. *Phil. Trans. R. Soc. B* 373, 20170120.
37. Schwarz, W., and Keus, I.M. (2004). Moving the eyes along the mental number line: Comparing SNARC effects with saccadic and manual responses. *Percept. Psychophys.* 66, 651–664.
38. Zorzi, M., Piffrits, K., and Umiltà, C. (2002). Neglect disrupts the mental number line. *Nature* 417, 138–139.
39. Piazza, M., Izard, V., Pinel, P., Le Bihan, D., and Dehaene, S. (2004). Tuning Curves for Approximate Numerosity in the Human Intraparietal Sulcus. *Neuron* 44, 547–555.
40. Eger, E., Michel, V., Thirion, B., Amadon, A., Dehaene, S., and Kleinschmidt, A. (2009). Deciphering Cortical Number Coding from Human Brain Activity Patterns. *Curr. Biol.* 19, 1608–1615.
41. Pearson, J.M., Hayden, B.Y., Raghavachari, S., and Platt, M.L. (2009). Neurons in Posterior Cingulate Cortex Signal Exploratory Decisions in a Dynamic Multioption Choice Task. *Curr. Biol.* 19, 1532–1537.
42. Hubbard, E.M., Piazza, M., Pinel, P., and Dehaene, S. (2005). Interactions between number and space in parietal cortex. *Nat. Rev. Neurosci.* 6, 435–448.
43. Piazza, M., and Eger, E. (2016). Neural foundations and functional specificity of number representations. *Neuropsychologia* 83, 257–273.
44. Viswanathan, P., and Nieder, A. (2013). Neuronal correlates of a visual “sense of number” in primate parietal and prefrontal cortices. *USA* 110, 11187–11192.
45. Ditz, H.M., and Nieder, A. (2015). Neurons selective to the number of visual items in the corvid songbird endbrain. *Proc. Natl. Acad. Sci. USA* 112, 7827–7832.
46. Kobylkov, D., Mayer, U., Zanon, M., and Vallortigara, G. (2022). Number neurons in the nidopallium of young domestic chicks. *USA* 119, e2201039119.
47. Harvey, B.M., and Dumoulin, S.O. (2017). A network of topographic numerosity maps in human association cortex. *Nat. Human Behav.* 1, 0036.
48. Harvey, B.M., Klein, B.P., Petridou, N., and Dumoulin, S.O. (2013). Topographic Representation of Numerosity in the Human Parietal Cortex. *Science* 341, 1123–1126.
49. Longo, M.R., and Lourenco, S.F. (2007). Spatial attention and the mental number line: Evidence for characteristic biases and compression. *Neuropsychologia* 45, 1400–1407.
50. Longo, M.R., Lourenco, S.F., and Francisco, A. (2012). Approaching stimuli bias attention in numerical space. *Acta Psychol.* 140, 129–132.
51. Casarotti, M., Michielin, M., Zorzi, M., and Umiltà, C. (2007). Temporal order judgment reveals how number magnitude affects visuospatial attention. *Cognition* 102, 101–117.
52. Galfano, G., Rusconi, E., and Umiltà, C. (2006). Number magnitude orients attention, but not against one’s will. *Psychon. Bull. Rev.* 13, 869–874.
53. Ristic, J., and Kingstone, A. (2006). Attention to Arrows: Pointing to a New Direction. *Q. J. Exp. Psychol.* 59, 1921–1930.
54. Fischer, M.H., Castel, A.D., Dodd, M.D., and Pratt, J. (2003). Perceiving numbers causes spatial shifts of attention. *Nat. Neurosci.* 6, 555–556.
55. Ranzini, M., Dehaene, S., Piazza, M., and Hubbard, E.M. (2009). Neural mechanisms of attentional shifts due to irrelevant spatial and numerical cues. *Neuropsychologia* 47, 2615–2624.
56. Dehaene, S. (1996). The Organization of Brain Activations in Number Comparison: Event-Related Potentials and the Additive-Factors Method. *J. Cognit. Neurosci.* 8, 47–68.
57. Göbel, S.M., Calabria, M., Farnè, A., and Rossetti, Y. (2006). Parietal rTMS distorts the mental number line: Simulating ‘spatial’ neglect in healthy subjects. *Neuropsychologia* 44, 860–868.
58. Dehaene, S., Piazza, M., Pinel, P., and Cohen, L. (2003). THREE PARIETAL CIRCUITS FOR NUMBER PROCESSING. *Cogn. Neurosci.* 20, 487–506.
59. Mora-Cortes, A., Gulbinaite, R., Ridderinkhof, K.R., and Cohen, M.X. (2023). Using the SSVEP to measure the SNARC-spatial attention effects in a parity judgment task. *Physiology*.
60. Corbetta, M., and Shulman, G.L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3, 201–215.
61. Posner, M.I., and Petersen, S.E. (1990). The Attention System of the Human Brain. *Annu. Rev. Neurosci.* 13, 25–42.
62. Bortot, M., Stancher, G., and Vallortigara, G. (2020). Transfer from Number to Size Reveals Abstract Coding of Magnitude in Honeybees. *iScience* 23, 101122.
63. Rugani, R., Zhang, Y., Ahmed, N., and Brannon, E. (2022). Children perform better on left than right targets in an ordinal task. *Acta Psychol.* 226, 103560.
64. Vallortigara, G. (2012). Core knowledge of object, number, and geometry: A comparative and neural approach. *Cogn. Neurosci.* 29, 213–236.
65. Edwards, L.A., Wagner, J.B., Simon, C.E., and Hyde, D.C. (2016). Functional brain organization for number processing in pre-verbal infants. *Dev. Sci.* 19, 757–769.
66. McCrink, K., Veggiotti, L., and de Hevia, M.D. (2020). A left visual advantage for quantity processing in neonates. *Ann. N. Y. Acad. Sci.* 1477, 71–78.
67. Longo, M.R., and Lourenco, S.F. (2007). Space perception and body morphology: extent of near space scales with arm length. *Exp. Brain Res.* 177, 285–290.
68. Loftus, A.M., Nicholls, M.E.R., Mattingley, J.B., Chapman, H.L., and Bradshaw, J.L. (2009). Pseudoneglect for the Bisection of Mental Number Lines. *Q. J. Exp. Psychol.* 62, 925–945.
69. Rugani, R., Platt, M.L., Chen, Z., and Brannon, E.M. (2022). Relative numerical middle in rhesus monkeys. *Biol. Lett.* 18, 20210426.
70. Aleotti, S., Di Girolamo, F., Massaccesi, S., and Piffrits, K. (2020). Numbers around Descartes: A preregistered study on the three-dimensional SNARC effect. *Cognition* 195, 104111.
71. Greenacre, L., Garcia, J.E., Chan, E., Howard, S.R., and Dyer, A.G. (2022). Vertical versus horizontal Spatial-Numerical Associations (SNA): A processing advantage for the vertical dimension. *PLoS One* 17, e0262559.
72. Cohenkadosh, R., Lammertyn, J., and Izard, V. (2008). Are numbers special? An overview of chronometric, neuroimaging, developmental and comparative studies of magnitude representation. *Prog. Neurobiol.* 84, 132–147.
73. Vallesi, A., Binns, M.A., and Shallice, T. (2008). An effect of spatial–temporal association of response codes: Understanding the cognitive

- representations of time. *Cognition* 107, 501–527.
74. Bonato, M., Zorzi, M., and Umiltà, C. (2012). When time is space: Evidence for a mental time line. *Neurosci. Biobehav. Rev.* 36, 2257–2273.
 75. Conson, M., Cinque, F., Barbarulo, A.M., and Trojano, L. (2008). A common processing system for duration, order and spatial information: evidence from a time estimation task. *Exp. Brain Res.* 187, 267–274.
 76. Bruzzi, E., Talamini, F., Priftis, K., and Grassi, M. (2017). A SMARC Effect for Loudness. *Iperception*. 8, 2041669517742175.
 77. Chang, S., and Cho, Y.S. (2015). Polarity correspondence effect between loudness and lateralized response set. *Front. Psychol.* 6, 683.
 78. Hartmann, M., and Mast, F.W. (2017). Loudness Counts: Interactions between Loudness, Number Magnitude, and Space. *Q. J. Exp. Psychol.* 70, 1305–1322.
 79. Ren, P., Nicholls, M.E.R., Ma, Y.y., and Chen, L. (2011). Size Matters: Non-Numerical Magnitude Affects the Spatial Coding of Response. *PLoS One* 6, e23553.
 80. Sellaro, R., Treccani, B., Job, R., and Cubelli, R. (2015). Spatial coding of object typical size: evidence for a SNARC-like effect. *Psychol. Res.* 79, 950–962.
 81. Dalmaso, M., and Vicovaro, M. (2019). Evidence of SQUARC and distance effects in a weight comparison task. *Cognit. Process.* 20, 163–173.
 82. Loconsole, M., Pasculli, M.S., and Regolin, L. (2021). Space-luminance crossmodal correspondences in domestic chicks. *Vis. Res.* 188, 26–31.
 83. Fumarola, A., Prpic, V., Da Pos, O., Murgia, M., Umiltà, C., and Agostini, T. (2014). Automatic spatial association for luminance. *Atten. Percept. Psychophys.* 76, 759–765.
 84. Peirce, J., Gray, J.R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., Kastman, E., and Lindeløv, J.K. (2019). PsychoPy2: Experiments in behavior made easy. *Behav Res* 51, 195–203.
 85. Albus, U. (2012). Guide for the Care and Use of Laboratory Animals (8th edn). *Lab. Anim.* 46, 267–268.
 86. Rugani, R., Platt, M.L., Chen, Z., and Brannon, E.M. (2020). Middle identification for rhesus monkeys is influenced by number but not extent. *Sci. Rep.* 10, 17402.

STAR★METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|-------------------------|-----------------------------|---|
| Deposited data | | |
| Raw and analyzed data | This paper | https://researchdata.cab.unipd.it/id/eprint/836 |
| Software and algorithms | | |
| PsychoPy3 | Peirce et al. ⁸⁴ | https://www.psychopy.org/ |
| R 4.0.3 | R Core Team | https://www.r-project.org/ |

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Rosa Rugani (rosa.rugani@unipd.it).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Data. Our data are stored and backed up on the Research Data Unipd server and are publicly accessible. The Research Data Unipd is Research Data Repository that meets the demands of a FAIR data storage (Findable, Accessible, Interoperable, Reusable) in accordance with the Guidelines on FAIR Data Management in Horizon 2020- July 2016; <https://researchdata.cab.unipd.it/id/eprint/836>.
- Code. Our codes for statistical analysis are stored and backed up on the Research Data Unipd server, and are publicly accessible. <https://researchdata.cab.unipd.it/id/eprint/836>.
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

All experimental procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of Pennsylvania and executed according to the "Guide to the Care and Use of Laboratory Animals"⁸⁵. The PROTOCOL # 806050 has been also revised by the Institutional Animal Care and Use Committee (IACUC) applying the expedited procedure set forth in 45 CFR 46.110 and approved on 05-Feb-2019.

Subjects

Two rhesus macaques (*Macaca mulatta*), a female named Sally (9 years old) and a male named Hooke (7 years old), served as subjects. The monkeys were housed in pairs in a vivarium and separated to participate in the experimental sessions. During testing, while one monkey performed the task, the other waited in an adjacent but separate area (usually Hooke took part at the daily test sessions as first). A grid separated the testing from the waiting area; however, it is unlikely that the waiting monkey could see the other monkey working as the grid only allowed for a partial view, and the working monkey positioned itself in front of the monitor, obstructing the view. Monkeys were provided with LabDiet's Monkey Diet biscuits, fresh vegetables, and fruits daily. Water was available *ad libitum*. This was the first touch screen study for both monkeys.

METHOD DETAILS

Apparatus, stimuli and procedure

The experimental apparatus consisted of a 15-inch touch-sensitive monitor (Elo TouchSystems, Menlo Park, CA) and a food pellet reward delivery system (Med Associates, St. Albans, VT). The monitor was attached to the front of the home cage. The reward delivery system was placed so that the food pellets dropped directly into the food box, located beneath the touchscreen. Stimulus presentation, reward delivery and data collection were performed with PsychoPy3.⁸⁴ The modality of presentation, the target stimulus and the number of the dots displayed on each trial depended on the experimental phase (see below). The position of every item was established by the position of its center on the two diagonals. We used a virtual Cartesian coordinate system with one centimeter as the standard unit. The origin of the coordinate was the center of the screen (0,0; which respectively indicate the position on the X and Y axes).

Shaping

Three shaping phases were designed to train monkeys to interact with the touchscreen by rewarding touches to the screen with increasing precision.^{69,86}

Shaping phase 1

We first shaped monkeys to touch a single blue dot (RGB = 0,0,255), randomly placed on the left/right, up/down location on the monitor. Because it was the first touch screen experience for both monkeys, the diameter of the dot was initially large (16cm), and it gradually halved in size, until it was 2cm. The size was reduced when the monkey completed two complete sessions of 32 trials on two consecutive days. Response time to touch the dot was unlimited. Whenever the dot was selected, the subject received a food pellet, a sound was played, and the screen turned green (RGB = 0,128,0) for 2 s. Once the monkeys completed two consecutive sessions without any pause between responding greater than 1 min, they moved to the subsequent shaping phase.

Shaping phase 2

We introduced a 2 × 2cm blue square as a start stimulus presented in the bottom-center of the monitor (0,-8) on every trial. Monkeys were required to touch the start stimulus to initiate each trial, and this served to anchor attention and standardize reaction-times across the experiment. After the start stimulus was touched, a 2cm blue dot was presented in one of 32 different screen locations, with the X and the Y coordinates varying randomly (1,-8). Once the monkeys completed two consecutive sessions without an interruption of greater than one minute, they moved to the subsequent shaping phase.

Shaping phase 3

Shaping PHASE 3 was identical to Phase 2 and thus required a response to the blue start square followed by a response to the single blue dot, but monkeys were required to make a response within 5 seconds to obtain reward. If a monkey did not respond within 5 seconds, the monitor turned black (RGB = 0,0,0) for 5 seconds and no reward was provided. Each session consisted of 64 trials and a performance criterion of 70% of valid trials over two consecutive sessions was required to advance to Training.

Training

After a correct response to the start stimulus, two 2cm dark gray dots (RGB = 47,79,79) were presented on a light gray (RGB = 211,211,211) background. At the same time, a picture of a green dinosaur (1.7 × 1.7cm) appeared over one of the two dots and remained until the monkey touched it. The general aim of Training was to shape monkeys to respond to a target stimulus and to memorize its location on the screen. To achieve this goal, Training was divided into 3 Phases (described below).

Training phase 1

After the start stimulus was touched, two 2cm dark gray dots were presented 11cm apart on the left (X = -6) and right (X = 6) side of the monitor. Although the position on the X axis was constant, their position on the Y axis varied from trial to trial (Y = -4,0,4). The same vertical jittering was also used in all subsequent training and testing. The dinosaur target stimulus was presented on the left or the right with equal frequency and remained on the screen until it was touched. An unlimited amount of time to respond was provided and only correct responses to the dot with the target stimulus were recorded and reinforced. Incorrect responses were ignored until the monkey made the correct response. Each Training Phase 1 session consisted of 60 trials. Once monkeys completed three consecutive sessions without a 1-min interruption they moved to Training Phase 2.

Training phase 2

The procedure followed all the same parameters as Training Phase 1, except that only correct responses were rewarded. If a monkey failed to respond within 5 seconds after initiating the trial or if the monkey made an incorrect response, the trial was ended with no reward and a 5-second black screen ensued. Each session consisted of 60 trials, and monkeys were moved to the subsequent training phase after two consecutive sessions of at least 80% correct responses.

Training phase 3

This training phase was designed to teach the monkeys to memorize the target's location. Training 3 was divided into five training phases in which the visibility of the target on the last screen (labeled *Recall screen*, Figure 1) was progressively reduced until it was no longer visible and thus required recall. In all phases of Training 3, monkeys were required to initiate trials by touching the start stimulus (Figure 1, *Start screen*), and were subsequently presented with two dark-grey dots one which displayed the dino target stimulus within its border. Monkeys were required to select the target stimulus within 5 seconds to continue the trial (Figure 1, *Target presentation and selection*). If the target was selected, both dots turned orange (RGB = 255,165,0) as shown in Figure 1 (*Intermediate screen*) for 3 seconds before disappearing. After 3-seconds elapsed the orange dots disappeared and were replaced with a transitional response square (a 2 × 2 cm orange square, located at 0,-8) until it was selected (Figure 1, *Attention relocation*). Once the monkey touched the transitional square, the two orange dots

reappeared (Figure 1, Recall screen). Monkeys were required to select the target stimulus within 5 seconds. An incorrect response or no response within 5 seconds resulted in the screen turning black for 5 seconds and no reward was delivered. In Training 3 phase 1, the dino target was fully visible in the recall screen. In Training 3 phase 2, the target opacity was reduced to .3 in the recall screen on all trials. In phase 3, the opacity was 0, .1, .2 or .3, with equal frequency in randomized order of presentation. In phase 4, the opacity was 0 on half of the trials and .1 on the other half, presented in random order. In phase 5, the opacity of the target stimulus was 0 on all trials requiring monkeys to recall the location of the target stimulus from earlier in the trial to obtain reward. In all training phases, the criteria for moving to the following phase was 80% accuracy over two consecutive sessions. Monkeys completed 60, phase 1, or 72 trials, phases 2–5, per session.

Number transfer tests

We then tested the monkeys with four transfer tests to explore whether they could remember the target location in arrays comprising a larger number of dots and to test whether monkeys exhibited a spatial bias. Specifically, we tested monkeys with arrays of 2, 4, 6, 10 identical dots. The experimental design was identical to phase 5 of Training 3, so that on the Recall screen the target was always invisible. The only differences consisted in the number of dots presented on each trial, their spacing, and the location of the target stimulus. On all transfer tests, correct responses were rewarded with a food pellet and a green screen and incorrect responses elicited no feedback. Each trial lasted for 10 s or until a correct response was made. Based on previous research using similar tasks and reinforcement procedures^{69,86} to maintain high motivation throughout the test, each subject underwent two consecutive test sessions on every testing day.

Two 2-dot test sessions were conducted (36 trials per session). In each trial, two dots appeared ($X = -2.8$ and 2.8 ; distance between dots 3.6 cm; overall length array = 7.6 cm); Figure 2A. The target stimulus randomly appeared on the left dot in half of the trials and on the right in the other half.

Two 4-dot test sessions were conducted (72 trials per session). The target stimulus appeared randomly 25% of the time in each position (1L; 2L; 1R; 2R), the distance was 3.6cm and the overall length of the array was 18.8cm; Figure 2B.

Two 6-dot test sessions were conducted (72 trials per session). The target stimulus appeared in each of four positions (2L; 3L; 2R; 3R) with equal frequency in a random order; Figure 2C. The inter dot distance was 3.6cm such that the overall array was 30cm.

Four 10-dot test sessions were conducted (54 trials per session). In each session, the target stimulus appeared randomly nine times on each of the following six positions (2L; 3L; 4L; 2R; 3R; 4R); Figure 2D. The inter dot distance was 1 cm and the overall length array was 29cm.

Conflict test

A 72-trial conflict test was conducted to disentangle whether monkeys used a numerical or spatial strategy. In the presentation phase, monkeys were presented with a 6-item array with the inter-dot distance held at 0.8cm and a 16 cm array length. As shown in Figure 4, the target appeared at 3L or 3R. In the recall phase, the spatial layout of the 6-item array was changed such that inter-item distance was 3.6cm, and the overall length was 30cm. As shown in Figure 4, this change meant that if the monkeys encoded the absolute spatial position of the targets they should choose 2L and 2R rather than 3L and 3R.

Continuous transfer test

In this test, we explored whether monkeys could transfer the training they had with discrete dots to solve a purely spatial version of the task. We conducted four sessions of 54 trials each. In presentation and recall phase of each trial, a single solid and continuous bar was presented instead of discrete dots. The bar was 2 cm high x 20 cm long and could be divided into 10 locations (each measuring 2×2 cm) with positions 1L–5L to the left of the midpoint and 5R–1R to the right of the midpoint. As shown in Figure 5, the target stimulus randomly appeared in one of three positions on the left ($X = -3, -5, -7$; respectively, labeled 2L, 3L, 4L) or on the right side ($X = 3, 5, 7$; respectively, labeled 2R, 3R, 4R) on the bar.

Data analysis was conducted using R 4.0.3. The stats, car, emmeans, rcompanion, and pwr packages were used to conduct analysis and calculate effect sizes. The Bonferroni correction was used for multiple comparisons. The first response on the recall frame of each trial was coded as 1(correct) or 0 (incorrect). Testing trials with no response were discarded from further analysis (5 trials, 0.295%). Additionally, computer errors resulted in 32 missing trials (22.22%) of the four-dot number transfer test for Hooke.

QUANTIFICATION AND STATISTICAL ANALYSIS

Data analysis was conducted using R 4.0.3. The stats, car, emmeans, rcompanion, and pwr packages were used to conduct analysis and calculate effect sizes. The Bonferroni correction was used for multiple comparisons. The first response on the recall frame of each trial was coded as 1(correct) or 0 (incorrect). Testing trials with no response were discarded from further analysis (5 trials, 0.295%). Additionally, computer errors resulted in 32 missing trials (22.22%) of the four-dot number transfer test for Hooke.